Flexible Establishment of Functional Brain Networks Supports Attentional Modulation of Unconscious Cognition

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Abstract: In classical theories of attention, unconscious automatic processes are thought to be independent of higher-level attentional influences. Here, we propose that unconscious processing depends on attentional enhancement of task-congruent processing pathways implemented by a dynamic modulation of the functional communication between brain regions. Using functional magnetic resonance imaging, we tested our model with a subliminally primed lexical decision task preceded by an induction task preparing either a semantic or a perceptual task set. Subliminal semantic priming was significantly greater after semantic compared to perceptual induction in ventral occipito-temporal (vOT) and inferior frontal cortex, brain areas known to be involved in semantic processing. The functional connectivity pattern of vOT varied depending on the induction task and successfully predicted the magnitude of behavioral and neural priming. Together, these findings support the proposal that dynamic establishment of functional networks by task sets is an important mechanism in the attentional control of unconscious processing. *Hum Brain Mapp* 35:5500–5516, 2014. © 2014 Wiley Periodicals, Inc.

Key words: automatic processes; fMRI; functional connectivity; masked semantic priming; subliminal perception

INTRODUCTION

A wide range of perceptual or cognitive processes can be triggered by stimuli that are presented outside of conscious awareness, a phenomenon also known as “subliminal perception” (Holender, 1986). Processing of unconsciously perceived stimuli is not restricted to the sensory or visuo-motor systems, but also extends to higher cognitive levels such as semantics (e.g., word meaning) or action control (e.g., mental operations) (Kiefer, 2012). An important

method to measure unconscious processes are subliminal priming (e.g., facilitatory) effects on subsequent decisions on visible targets, which are elicited by masked visual stimuli that are not consciously perceived (Dehaene et al., 1998; Greenwald et al., 1996; Kiefer, 2002; Vorberg et al., 2003). For instance, a pattern mask consisting of random letters is presented after the prime to prevent its conscious perception (Breitmeyer and Ögmen, 2006). Although masked prime stimuli cannot be consciously identified, they elicit priming effects indexing cognitive processes at several levels of complexity (for reviews, see Ansorge et al., 2011; Dehaene et al., 2006; Kiefer et al., 2011; Kunde et al., 2012; Schmidt et al., 2011).

Even unconscious analysis of word meaning has been reliably demonstrated (Kiefer, 2002; Kiefer and Spitzer, 2000): Lexical decisions (word/pseudoword classifications) are faster and the N400 component of the event-related potential is smaller when the target word is preceded by a semantically related (R) masked prime word (e.g., table-chair) compared with a semantically unrelated (U) one (e.g., bottle-rock). A recent neuroimaging study related

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this subliminal semantic priming effect to reduced activation of the ventral occipito-temporal region (vOT) including the fusiform gyrus (Ulrich et al., 2013) which is also involved in priming elicited by visible prime words (Gold et al., 2006; Ulrich et al., 2013; Wheatley et al., 2005). This region within the ventral visual pathway has been associated with the representation of semantic features (e.g., Chao et al., 1999; Martin and Chao, 2001; Martin et al., 1995), which are automatically activated in response to a meaningful word, even when presented outside visual awareness.

Supraliminal semantic priming, which also involves controlled semantic mechanisms such as a comparison of the meaning of the prime and the target word (semantic matching) in addition to automatic semantic processing (Neely, 1991), modulated activity also in brain regions other than vOT. The regions varied widely across studies and included the superior and the middle temporal gyri (Copland et al., 2003; Giesbrecht et al., 2004; Gold et al., 2006; Kotz et al., 2002; Matsumoto et al., 2005; Rissman et al., 2003; Wible et al., 2006), as well as the inferior and the middle frontal gyri (Copland et al., 2003; Giesbrecht et al., 2004; Kotz et al., 2002; Matsumoto et al., 2005; Rissman et al., 2003; Wheatley et al., 2005; Wible et al., 2006). It has therefore been suggested that vOT reflects automatic semantic activation whereas other temporal and frontal areas support controlled semantic processing (Ulrich et al., 2013).

Traditionally, automatic processes such as unconscious semantic activation are thought to operate autonomously, and not amenable to attentional top-down modulation (Heil et al., 2004; Neely and Kahan, 2001; Posner and Snyder, 1975; Schneider and Shiffrin, 1977). A meaningful stimulus such as a word should invariantly trigger activation in semantic pathways. According to this traditional view, only conscious processes are susceptible to attentional control (Posner and Snyder, 1975; Schneider and Shiffrin, 1977).

Recently, the classical notion of autonomous automatic processing has been challenged on the basis of findings showing that unconscious automatic processes do depend on capacity-limited spatial, and temporal attention (e.g., Kentridge et al., 2004; Kiefer and Brendel, 2006; Naccache et al., 2002) or action intentions (Ansorge and Neumann, 2005). As a unifying account for a variety of top-down influences such as attention, intention, and task sets, Kiefer and Martens (2010) proposed the attentional sensitization model of unconscious cognition that extends previous frameworks of attention from the conscious (e.g., Miller and Cohen, 2001) to the unconscious domain. The model holds that task sets represented in prefrontal cortex sensitize task-relevant, and desensitize task-irrelevant processing pathways, thereby influencing not only the conscious, but also the unconscious information flow: By means of this preemptive control mechanism, subliminal information should be processed only along the sensitized processing pathways. In order to test these predictions, the

induction task paradigm was developed, in which the subliminally primed lexical decision task is preceded by a semantic induction task, for example, semantic classification of objects or words, as compared to perceptual induction, for example, shape classification of objects or letters, or phonological induction, for example, phonological classification of letters (Adams and Kiefer, 2012; Kiefer and Martens, 2010; Martens et al., 2011). In line with the attentional sensitization model, unconscious semantic priming effects were boosted, when a semantic task set was active during masked prime presentation, whereas an active perceptual or phonological task set attenuated or abolished unconscious semantic priming. Importantly, for subliminal visuo-motor priming, which should benefit from a sensitization of perceptual shape processing pathways, the opposite pattern was observed: Visuo-motor priming was enhanced by an activated perceptual shape task set, but abolished by a semantic task set (Martens et al., 2011). These behavioral and electrophysiological studies clearly demonstrate that even unconscious processing is under attentional control to some extent. Despite this converging evidence, the neural mechanisms underlying attentional modulation of unconscious cognition have not been determined yet.

Here, we propose that attentional sensitization of unconscious cognition is implemented by a dynamic modulation of the functional communication between brain regions. This novel dynamic functional networks framework builds upon the broader idea that the function of a given brain region is determined by its temporary, dynamic functional coupling with other brain regions (cf., Bressler and Kelso, 2001). Currently activated task sets may impact the unconscious information flow in neural processing pathways by temporarily establishing different functional networks (see also Heinzle et al., 2012; Sakai and Passingham, 2003). This proposal implies that the function of a given brain region may change in dependence of its dynamic integration into large-scale brain networks. Most likely, these temporary functional networks are established by attentional task sets through a modulation of the phase-locking of oscillatory neural activity, that is, coherence (Fries, 2005), across distant brain areas (cf., Womelsdorf and Fries, 2007).

In the present study, we tested this proposed mechanism underlying attentional control of unconscious cognition by measuring brain activation and functional connectivity with functional magnetic resonance imaging (fMRI) during masked semantic priming under different task sets. We utilized the induction task paradigm (Kiefer and Martens, 2010; see Fig. 1) consisting of a subliminally primed visual lexical decision task preceded by a semantic or a perceptual induction task. To induce a semantic task set, pictures had to be classified according to whether they referred to living versus nonliving objects, whereas the perceptual induction task required decision on the shape of objects (round vs. elongated shape). Please note that in the present and earlier experiments task sets associated

Figure 1.

Schematic overview of the experimental paradigm. On each trial, the object depicted on the induction image had to be classified according to animacy (living/nonliving in the semantic induction task) or to shape (round/elongated in the perceptual induction task), thereby inducing a semantic or a perceptual task set, respectively. Following the induction task a subliminally primed lexical decision task required subjects to decide whether or not the target was a word. The induction tasks were performed in separate fMRI sessions. ITI: intertrial interval.

with the induction tasks are set up consciously by the participants, but are expected to influence subsequent unconscious prime processing. This has to be distinguished from other studies using masked (invisible) cues to trigger task sets unconsciously (e.g., Lau and Passingham, 2007; Matzler, 2003).

We found neural semantic priming, defined as less brain activation associated with related compared with unrelated trials, in a vOT region known to be involved in semantic processing (Gold et al., 2006; Ulrich et al., 2013; Wheatley et al., 2005) only subsequent to semantic, but not subsequent to perceptual induction. Furthermore, during the semantic induction task, vOT exhibited stronger functional connectivity with a brain region implicated in semantic processing (superior frontal gyrus). In contrast, during the perceptual induction task vOT was more strongly coupled with regions known to be involved in visual shape processing (occipital and temporal regions).

Most importantly, the induction task-dependent differential functional connectivity pattern of vOT significantly predicted the magnitude of behavioral and neural subliminal semantic priming. In support of the dynamic functional networks theory, this result pattern shows that attentional control of unconscious cognition is achieved by dynamically coupling brain areas into different large-scale functional networks.

MATERIALS AND METHODS

Participants

Twenty-three students (13 female) aged 21.1 years on average (standard deviation (SD) = 2.6) were recruited from the local university and were paid 25 EUR for participation. All of them were right-handed German native speakers. Neither psychiatric nor neurological diseases nor any contraindications regarding the fMRI procedure were reported. Written informed consent was obtained prior to the experimental phase. The study has been approved by the ethics committee at the University of Ulm and was conducted in accordance with the Declaration of Helsinki.

Stimuli

For the semantic (Sem) and the perceptual (Per) induction tasks, stimuli from our previous investigations were used (Kiefer and Martens, 2010, Experiment 3; Martens et al., 2011, Experiment 1). Stimuli were 240 gray-scale images depicting either living-round, living-elongated, nonliving-round, or nonliving-elongated objects. Two sets of induction images were formed, each with a balanced amount of the four image types. The first set was used for the semantic induction task where objects had to be classified with regard to animacy (living vs. nonliving) whereas the second set was used for the perceptual induction task which required a decision on the shape of the object (round vs. elongated). From a pilot study (for details, see Kiefer and Martens, 2010) reaction times associated with each image upon semantic, or perceptual decision, respectively, were available. Reaction times did not significantly vary as a function of image set (= induction task) or image type as evidenced by an analysis of variance (ANOVA), neither attesting significance to the main effects (image set: $F(1, 232) = 0.03$, $P = 0.875$; image type: $F(3, 232) = 0.92$, $P = 0.432$) nor to the interaction between the two factors ($F(3, 232) = 0.70$, $P = 0.556$).

Primes and targets used for the lexical decision task were also taken from previous studies (Kiefer, 2002; Kiefer and Martens, 2010; Kiefer and Spitzer, 2000). Stimuli consisted of German words (nouns, verbs, adjectives) and pronounceable pseudowords, with the latter derived from regular German words by changing one or two letters to make them meaningless. Pseudowords were used as distracters for the lexical decision task, but not further

analyzed. Two stimulus lists were created, each containing 30 word-word pairs related in meaning (R) (e.g., fork-knife), 30 word-word pairs unrelated in meaning (U) (mouth-garden), and 60 word-pseudoword pairs (P). The first word of each pair was later used as prime and the second item as target. Stimuli were matched for average word length and frequency (Ruoff, 1990) within and across lists (confirmed by non-significant interactions in four "stimulus list" by "event type" ANOVAs: $\text{length}_{\text{prime}}: F(2, 234) = 0, P = 1$; $\text{length}_{\text{target}}: F(2, 234) = 0.02, P = 0.983$; $\text{frequency}_{\text{prime}}: F(2, 234) = 0, P = 1$; $\text{frequency}_{\text{target}}: F(1, 116) = 0, P = 1$). As we were mainly interested in interactions between induction task and semantic relatedness, any possible unnoticed insufficient matching of word lists does not affect the interpretation of our findings.

In order to obtain a sequence of R, U, and P trials allowing for efficient estimation of the associated hemodynamic responses, the program "Optseq2" (<http://surfer.nmr.mgh.harvard.edu/optseq/>; see also Dale, 1999) was employed. Trial order and trial onsets as initially delivered by the program were modified such that a specific trial type did not appear more than three times in direct succession. Furthermore, onsets were jittered by randomly adding fractions of the fMRI repetition time (TR). The resulting average trial onset asynchronies were 35.5 s for R trials and 37.0 s for U trials, not significantly differing from each other ($t(56) = 0.27, P = 0.557$), and 18.6 s for P trials. The mean intertrial interval (ITI) averaged across all trials irrespective of event type was 5.7 s.

The two induction image sets and the two prime-target lists were combined in all possible ways. For each of the four combinations, the induction images were carefully assigned to the prime-target pairs such that within each image-prime-target triplet the induction image was semantically unrelated to the prime and to the target. Furthermore, the four types of induction images (e.g., living-round, living-elongated, etc.) were balanced within each event type (R, U, and P), as well as across R and U, and across the four combinations of image set and prime-target list, in order to rule out any effects of response congruency between induction task and lexical decision task. The image-prime-target triplets were then pseudo-randomly assigned to the optimized sequence of R, U, and P trials described above, individually for each of the four combinations of image set and prime-target list. During the assignment it was ensured that a particular decision alternative in the induction task (e.g., "living" under Sem) did not repeat more than three times in direct succession, and that two and three consecutive repetitions occurred equally often for each decision alternative and induction task across all four combinations of image set and prime-target list.

Stimuli appeared on MRI compatible video goggles (VisuaStim Digital, Resonance Technology Inc., Northridge, CA, USA). If necessary, correction lenses were provided to ensure sufficient visual acuity. Resolution was set to 800×600 pixels and screen refresh frequency was set

to 60 Hz (frame duration = 16.67 ms; stimulus presentation and screen refreshes were synchronized). The induction images had a native resolution of 170 pixels in width and 216 pixels in height and subtended visual angles of 20.7° vertically and 12.2° horizontally. Primes and targets appeared in white 24-point IBM8BIT font against black background in the center of the display and spanned a visual angle of 2.3° vertically and, depending on (pseudo)-word length, $2.6^\circ - 10.5^\circ$ horizontally. All primes and targets were held in lowercase except for the first letter of nouns and of pseudonouns to conform to German orthography. Visual stimulation and recording of reaction times upon the lexical decision task (starting from target onset) was performed using Experimental Run Time System 3.35 (BeriSoft Cooperation, Frankfurt/Main, Germany) running under DOS 7.1 on a standard PC.

Procedure

In the run-up to the experiments, subjects were carefully instructed and trained. In the scanner, participants laid supine, with their head resting in foam padding to reduce head movements. Both induction task conditions, Sem and Per, were performed in two separate fMRI sessions, with session order counterbalanced across subjects. The four stimulus sets corresponding to 30 R, 30 U, and 60 P trials each were also counterbalanced across subjects such that each stimulus was presented only once to each participant.

The trial structure which is shown in Fig. 1 was the same for all event types, with a total duration of 3,517 ms. Participants first viewed a fixation cross lasting 750 ms, which was replaced by an induction image with 500 ms duration before the screen turned black for 500 ms. In the case of the semantic induction task, participants had to decide whether or not the presented object referred to a living object and to indicate their decision by pressing the left (living) or the right button (nonliving) of a self-built MRI compatible keyboard with their right index or middle finger, respectively. In the perceptual induction task, the object had to be classified according to its shape (right index finger: round; right middle finger: elongated). Subjects were asked to give the decision within 1,000 ms starting from onset of the induction image. A trial proceeded with a subliminally primed visual lexical decision task (Meyer and Schvaneveldt, 1971). Following the black screen, which completed the induction task, a forward pattern mask consisting of ten randomly drawn upper case letters was presented for 200 ms in the center of the screen. After disappearance of the mask, a prime word was presented for 33 ms. The prime was replaced by a backward pattern mask lasting 33 ms consisting of a new random letter set. Then, the target was presented with a duration of 500 ms, resulting in a prime-target stimulus onset asynchrony of 67 ms. Participants were asked to decide whether or not the target was a German word and to indicate their decision by pressing the left or the right

button with their right index or middle finger, respectively. The response was to be given within a time window of 1,500 ms beginning with target onset. After offset of the target three centered hash marks were presented for 1,000 ms (completing the trial), and they also persisted during a subsequent, variable ITI (mean = 5.7 s, maximum = 20.4 s). All responses were instructed to be given as fast and as accurate as possible, and participants were not informed about the presence of the masked prime. Instead, they were prepared to only see a “random letter string” prior to target presentation. At the beginning and at the end of the fMRI session, a fixation cross was shown for 13.2 s and 22.0 s, respectively, to account for scanner equilibration and to capture the hemodynamic response associated with the last trial.

Prior to each fMRI session, subjects performed a practice run which was divided into three blocks. First, participants practiced the induction task at hand with 10 trials (Sem: $5 \times \text{living}/5 \times \text{nonliving}$, Per: $5 \times \text{round}/5 \times \text{elongated}$) which began with a fixation cross (750 ms), followed by an induction image (500 ms) and a black screen (500 ms) before visual feedback was given (“correct” in green, and “wrong” or “faster” in red font). Second, subjects completed eight trials of an unprimed version of the lexical decision task (750 ms fixation, 500 ms target item, 1,000 ms hash marks, followed by feedback; targets: 4 words, and 4 pseudowords). In a third block, the induction task and a subliminally primed version of the lexical decision task were combined such that the trial structure corresponded to that of the main experiments as described above, except for additional feedback given after the induction task and after the lexical decision task. Participants performed 40 trials ($10 \times \text{R}$, $10 \times \text{U}$, $20 \times \text{P}$), with decision alternatives (e.g., “round” vs. “elongated” under Per) balanced within each event type. The stimulus material of the practice runs did not overlap with the stimulus sets used in the main experiments.

The scanning session ended with acquisition of a T1-weighted structural image of the brain. After scanning, still inside the scanner but offline, participants were informed about the presence of the primes. None of the participants reported to have seen the primes between the masks. Then, instructions on an additional task, which tested prime visibility objectively, were administered. For this test, in half of the trials a word (33 ms) appeared that had originally been used as prime in the main experiments. During the other half of the trials, a letter string consisting of seven repetitions of a randomly drawn upper case letter (33 ms) was shown (e.g., AAAAAAA). In both cases the stimulus was presented between a forward mask (133 ms) and a backward mask (33 ms), consisting of ten different, randomly drawn upper case letters as in the main experiments. The second item of a trial was always a word (no pseudowords) taken from the main experiment but no response had to be given here. This context word was presented at the position of the lexical decision target in the main experiment in order to keep stimulation com-

parable. Subjects were told to concentrate on the masks and to indicate by button press whether a word (right index finger) or a repeated letter string (right middle finger) had been presented between the masks. Emphasis was on accuracy over speed. Execution of the task was self-paced to ascertain that subjects felt optimally prepared before starting each trial. The visibility test had two blocks with 40 word trials and 40 repeated letter string trials each. In the first block, the words corresponded to a subset of the primes ($20 \times \text{R}$, and $20 \times \text{U}$) that subjects had encountered during the first fMRI session (e.g., Sem) whereas the second block featured primes shown in the second fMRI session (e.g., Per). Trials were presented in random order. Just before each block participants had to undergo ten practice trials (5 word trials, and 5 repeated letter string trials).

MRI Data Acquisition

Functional images were acquired on a 3 Tesla magnetic resonance scanner (Magnetom Allegra, Siemens AG, Erlangen, Germany) in combination with a single channel transmit/receive head coil (RAPID Biomedical GmbH, Rimpar, Germany). During the experimental runs, an echo-planar pulse sequence (EPI) was applied to measure the T2*-weighted blood oxygen level dependent (BOLD) signal. The following parameters were used: TR = 2,200 ms, echo time (TE) = 39 ms, flip angle = 90° , field of view (FOV) = 230 mm, matrix size = 64×64 , number of slices = 34, slice thickness = 3.0 mm, interslice gap = 0.6 mm, isotropic voxel size of 3.6 mm^3 . Ascending slice acquisition was parallel to a tangent plane touching the inferior surfaces of the orbitofrontal cortex and the cerebellum. Scan time per experimental run was 1,146 s, corresponding to 519 EPI volumes. To obtain a high resolution T1-weighted structural image for later coregistration purposes, a magnetization prepared rapid acquisition gradient echo sequence was employed (TR = 2,080 ms, TE = 3.93 ms, inversion time = 1,100 ms, flip angle = 12° , FOV = 256 mm, matrix size = 256×256 , voxel volume = 1 mm^3 , slice orientation: sagittal; scan time = 467 s).

Data Analysis

Behavioral data

Responses obtained from the lexical decision task were analyzed for reaction times (RT) and errors. Pseudoword trials were of no interest and not further analyzed. For RT analysis only correct lexical decisions were included within three standard deviations from the individual mean (across R and U) to protect against possible outliers. Individual mean RT data for R and U trials were fed into a 2×2 repeated measures ANOVA with factors induction task (Sem vs. Per) and semantic relatedness (R vs. U).

From the responses given in the two blocks of the prime visibility test corresponding to Sem and Per, d' (Green and Swets, 1966) was calculated by transforming the respective

false alarm rate for words (collapsed across R and U primes) into a z score which was subtracted from the z score pertaining to the corresponding hit rate. Separately for Sem, and for Per, the subject-wise d' values were tested for significant deviation from zero using one sample t tests. A paired-sample t test was used to test for significant difference in d' between Sem and Per.

The significance level was set to $P < 0.05$ for all statistical tests.

MRI data

Imaging data preprocessing and statistical analyses were performed with the software package Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, London, UK). Preprocessing started with slice timing correction and spatial realignment of the EPIs of each session to the session mean. Afterwards, images of each session were aligned to each other by coregistering the two mean EPIs and applying the resulting parameters to the images of the second session (either Sem or Per due to counterbalancing). Thereafter, the individual T1 image was coregistered to the mean EPI of the first run. The T1 image was then segmented into grey and white matter using SPM8's "new segment" routine. Spatial normalization to the Montreal Neurological Institute (MNI) space was achieved by applying the resulting individual deformation field to the T1 image and all EPI images. In that step, voxels were also resampled to a spatial resolution of isotropic 1.5 mm^3 . Finally, experimental EPI time series were smoothed using a Gaussian kernel with 8 mm full width at half maximum.

After data preprocessing, a hierarchical standard modeling approach was used. For each subject a session separated General Linear Model was set up with onsets for each condition of correct R, U, and P trials (beginning with the onset of the 750 ms fixation period). Please note that, due to the short time interval between the induction task and the lexical decision task, which is an essential methodological aspect of the induction task paradigm, and due to the slow time course of the hemodynamic response, it was not possible to model both tasks by separate regressors. Thus, theoretically the induction task might have affected lexical decisions for R and for U differentially, which, in turn, might have mimicked priming, that is, the difference "U minus R". However, this is very unlikely since the timing schedule of the induction task as well as that of the lexical decision task were identical for R, and for U trials. Given that R and U trials were indistinguishable until the target word had been processed, brain activity associated with the induction task can be assumed to have been of comparable magnitude and therefore been subtracted out. Thus, any observed differences in brain activity between R, and U likely had their basis in the lexical decision task, rather than in the induction task. As conditions of no interest, onsets of incorrect lexical decisions were added to the design matrix as were the spatial

realignment parameters. Resulting stick functions were convolved with the canonical hemodynamic response function and its time and dispersion derivatives. To remove low-frequency scanner drifts, data were high-pass filtered with a frequency cutoff at 128 s, and an autoregression model of polynomial order 1 was used to account for temporally correlated residual errors. Upon model estimation, contrast images representing the main effects "canonical R > implicit baseline" and "canonical U > implicit baseline" were created for both sessions (Sem, and Per) and entered into a random-effects analysis, implemented as flexible factorial design. The interaction "induction task" by "semantic relatedness" was specified as a single factor with four levels (R_{Sem} , U_{Sem} , R_{Per} , U_{Per}) by concatenating the two underlying factors. A second factor modeled the subject related variance. After estimation, two one-sided t contrasts were computed to test for significant neural priming effects specific to each induction task ($[U_{\text{Sem}} \text{ minus } R_{\text{Sem}}]$, and $[U_{\text{Per}} \text{ minus } R_{\text{Per}}]$). Another contrast examined the interaction between induction task and semantic relatedness, that is, greater neural semantic priming subsequent to the semantic than to the perceptual induction task ($[U_{\text{Sem}} \text{ minus } R_{\text{Sem}} \text{ minus } U_{\text{Per}} \text{ plus } R_{\text{Per}}]$). In order to ensure meaningful interpretation of possible interaction effects, the interaction contrast was restricted to those voxels for which significant neural priming effects had been demonstrated under Sem. Statistical parametric maps were assessed at a voxel height threshold of $P < 0.001$ and a family-wise error corrected cluster threshold of $P < 0.05$. Owing to the absence of significant priming under Per, a contrast testing for greater priming after perceptual than semantic induction, was not computed. Since presentation order of the induction task sessions was counterbalanced across participants, order of R and U trials within sessions was randomized, and MR data were high-pass filtered, potential scanner drifts could not have compromised BOLD activation analyses as well as functional connectivity analyses described below.

As one of the results of the interaction analysis, greater semantic priming under Sem than under Per was revealed for a cluster in left ventral occipito-temporal cortex. To test the prediction that this induction task-dependent modulation of neural semantic priming in vOT arose from its integration into distinct functional brain networks associated with either induction task, we performed context-dependent functional connectivity analyses using psychophysiological interactions (Friston et al., 1997; McLaren et al., 2012). In contrast to simply correlating two brain regions' signal time courses, a standard PPI model (Friston et al., 1997) includes the time course of the seed region of interest, the main effect of the psychological variable (context), and the interaction term between the two. PPI determines voxels in the brain, whose time courses are correlated with the seed region's time course in dependence of the psychological context after accounting for the main effects of time course and psychological context. Thus, PPI identifies brain regions whose activity is temporally coupled with that of the seed region

independent of their absolute activity level. For the standard PPI approach as implemented in SPM8 it is advantageous when the psychological variable varies within one and the same experimental fMRI run. In the present study, however, the psychological variable is “induction task”, the two levels of which were distributed across two different runs. We therefore employed the recently developed generalized form of context-dependent psychophysiological interactions (gPPI, McLaren et al., 2012; <http://www.nitrc.org/projects/gppi>) which provides more flexibility in that regard. For each participant, we individually defined the voxel bearing the highest induction task-by-semantic relatedness interaction within the left vOT cluster obtained in the group analysis as seed. Using this method of seed voxel definition we attempted to account for recent findings of high interindividual variability in resting state functional connectivity (Fox et al., 2013; Mueller et al., 2013). In our study, defining seed voxels based on the coordinates of the group analysis yielded a similar connectivity pattern compared with individually defined seeds, although cluster sizes and peak voxel-based effect sizes were smaller in almost all clusters (data not shown). Therefore, we report only the functional connectivity results obtained with the individually defined seeds. Conditions of interest for which PPI regressors were created were R and U under both induction tasks. Other regressors included in the model represented task-related activation associated with R, U, P, and incorrect lexical decision trials, the seed time course, and the realignment parameters. After model estimation, single-subject *t* contrasts representing functional connectivity with vOT associated with R, and U, under Sem, and under Per, were computed and subjected to a random-effects analysis implemented as flexible factorial design. Two one-sided *t* contrasts were set up to test for greater connectivity with left vOT under Sem than under Per, and vice versa ($[R_{\text{Sem}} \text{ plus } U_{\text{Sem}} \text{ minus } R_{\text{Per}} \text{ minus } U_{\text{Per}}]$, and $[R_{\text{Per}} \text{ plus } U_{\text{Per}} \text{ minus } R_{\text{Sem}} \text{ minus } U_{\text{Sem}}]$). Please note that these contrasts compared connectivity estimates averaged across R and U between both induction tasks. The rationale was that our theoretical focus rested on functional connectivity changes elicited by the induction tasks. Furthermore, we did not expect a modulation of the functional connectivity profile associated with the induction tasks by the subsequent R and U conditions. The resulting statistical parametric maps were thresholded at $P < 0.001$ at the voxel level, and it was further required that clusters exceeded SPM8’s expected cluster size of $k = 52$ contiguous voxels.

To assess the effect of induction task-specific functional connectivity with left vOT on modulation of behavioral, and of neural priming, correlation analyses were performed. In general, all correlation analyses were conducted voxel-wise, and were restricted to the clusters appearing in the functional connectivity group analysis described above. First, depending on the contrast by which the clusters had been revealed (Sem minus Per, or Per minus Sem), the individual “Sem minus Per”, or “Per minus Sem” difference in functional connectivity with left vOT was correlated with participants’ Sem minus Per difference

in RT priming (i.e., priming_{Sem} minus priming_{Per}). Similarly, the induction task-associated functional connectivity differences were correlated with the subject-wise Sem minus Per difference in neural semantic priming. Before that, the neural priming differences had been obtained in the following manner. First, beta estimates were extracted from all voxels of clusters that had, in terms of functional activation, demonstrated significantly greater neural semantic priming after semantic relative to perceptual induction. Then, subject-wise, the difference “U_{Sem} minus R_{Sem} minus U_{Per} plus R_{Per}” was calculated and averaged across all voxels of a given cluster. These averaged values were then entered into the aforementioned correlation analyses.

RESULTS

Behavioral Data

After the main experiment, a prime visibility test was performed, which required subjects to decide whether the item presented between two masks was a word or a string of repeated letters. The mean overall hit rates across words and repeated letter strings were 52.8 % under Sem and 50.7 % under Per, ranging from 42.5 % to 62.5 % in both conditions. Although one-sample *t* tests revealed a significant deviation from chance level for Sem ($t(22) = 2.78$, $P = 0.011$) but not for Per ($t(22) = 0.56$, $P = 0.581$), the hit rates associated with Sem and Per did not significantly differ from each other ($t(22) = 1.45$, $P = 0.160$). The *d'* measure of prime visibility (Green and Swets, 1966), was 0.15 on average (range: -0.38 to +0.65) under Sem and significantly deviated from zero ($t(22) = 2.79$, $P = 0.011$). In the Per condition mean *d'* was 0.03 (range: -0.40 to +0.64) and not significantly different from zero ($t(22) = 0.56$, $P = 0.583$). Again, the difference in *d'* between Sem and Per conditions was not significant ($t(22) = 1.48$, $P = 0.153$). Furthermore, RT semantic priming (see below) under Sem and Per, respectively, did not significantly correlate with identification accuracy or *d'* (all $t(21) < 1.32$, all $P > 0.201$). In summary, although we cannot completely rule out the possibility that the primes were marginally visible under Sem, it is unlikely that participants were able to recognize the words, given that identification measures were low and did not correlate with priming. Furthermore, participants did not report subjective visibility in the post-experimental debriefing (see the Methods section). Most importantly, as prime detection did not significantly differ between Sem and Per, any differences in semantic priming between the induction tasks can unlikely be accounted for by potential residual conscious prime identification.

After removal of outlying responses in the primed lexical decision task (Sem: 1.4 %, Per: 1.3 %), the following mean reaction times for correct trials were obtained (SD in brackets): R_{Sem}: 629 (64) ms, U_{Sem}: 651 (68) ms, R_{Per}: 631 (69) ms, U_{Per}: 644 (71) ms. A repeated measures ANOVA

Figure 2.

Brain regions showing significant neural priming, that is, less brain activation upon related relative to unrelated trials, following the semantic induction task. Effects were overlaid on coronal sections of the group averaged T1 image using MRIcron (<http://www.mccauslandcenter.sc.edu/mricro/mricron/>). Numbers in white color denote the y-coordinates of the coronal sections in MNI space. On the left and on the right, averaged parameter

estimates are depicted, representing neural activity associated with related, and unrelated trials after semantic (Sem), and perceptual (Per) induction. Estimates were extracted from and averaged across the entire respective cluster listed in Table I. Error bars represent standard error of the mean (23 subjects). Abbreviations: a.u.: arbitrary unit, L: left, R: right, IFG: inferior frontal gyrus, vOT: ventral occipito-temporal cortex.

on mean RT revealed significant semantic priming, that is, faster responses to related than to unrelated targets (main effect of relatedness, $F(1, 22) = 27.44$, $P < 0.001$). In accordance with previous work (Kiefer and Martens, 2010; Martens et al., 2011), semantic priming was numerically greater after semantic than perceptual induction (U-R difference: Sem: 22 ms, Per: 12 ms) although the interaction between induction task and semantic relatedness was not significant ($F(1, 22) = 1.51$, $P = 0.232$), presumably due to a relatively high variability of RT in the MR environment. Error rates (mean = 5.8 %) were generally low and not further analyzed.

Neuroimaging Data

Neural subliminal semantic priming as a function of induction task

Subsequent to the semantic induction task, semantic relatedness modulated the BOLD signal in a network of brain regions (see Fig. 2 and Table I) known to be involved in unconscious semantic processing (Ulrich et al., 2013). Significant semantic priming effects (greater activity

for U than for R) were found in left and right vOT clusters covering portions of the fusiform gyrus (FFG; Brodmann area (BA) 19/37), of the inferior temporal gyrus (ITG; BA 37), and of the inferior occipital gyrus (IOG; BA 19). The right vOT cluster additionally extended into the lingual gyrus (LG; BA 17/18), and the middle temporal gyrus (MTG; BA 21). The right middle occipital gyrus (BA 19) was also sensitive to priming under semantic induction. Priming effects were also observed in bilateral frontal areas. The left-hemisphere cluster comprised subdivisions of the precentral gyrus (BA 4), of the posterior inferior frontal gyrus (IFG, opercular part; BA 44), of the anterior IFG (triangular part; BA 45), and of the anterior insula. In the right hemisphere, a homologous, albeit smaller, cluster emerged, consisting solely of the anterior and the posterior IFG (BA 45, and 44, respectively). Priming effects under semantic induction were also found in the left hippocampus and in an adjacent portion of the amygdala.

In contrast, neural semantic priming after induction of a perceptual task set was not detected at the required statistical threshold. Even when not correcting for multiple comparisons at the cluster level, no significant clusters emerged.

TABLE I. Brain regions demonstrating subliminal semantic priming subsequent to the semantic induction task

Region	BA	Number of voxels	Peak voxel			
			<i>x</i>	<i>y</i>	<i>z</i>	<i>z</i> score
R Cerebellum	–	3,671	11	–78	–30	5.17
R Lingual gyrus	17		11	–88	–3	4.71
R Lingual gyrus	18		20	–81	–12	4.57
R Middle temporal gyrus	21		63	–34	–6	3.99
R Fusiform gyrus	19		38	–73	–20	3.93
R Inferior temporal gyrus	37		48	–52	–12	3.83
R Inferior occipital gyrus	18		36	–84	–11	3.74
L Inferior frontal gyrus opercular part	44	2,809	–44	15	12	4.64
L Anterior Insula	–		–29	26	10	4.61
L Inferior frontal gyrus triangular part	45		–32	27	12	4.14
L Precentral gyrus	4		–45	–4	31	4.08
R Inferior frontal gyrus triangular part	45	805	41	24	22	4.58
R Inferior frontal gyrus opercular part	44		44	8	25	3.43
R Inferior frontal gyrus triangular part	45		54	39	12	3.26
L Fusiform gyrus	37	1,596	–33	–45	–15	4.53
L Fusiform gyrus	37		–41	–58	–15	4.47
L Inferior temporal gyrus	37		–50	–57	–14	4.27
L Cerebellum	–		–38	–57	–23	3.80
L Inferior occipital gyrus	19		–29	–79	–14	3.48
R Middle occipital gyrus	19	727	32	–66	31	4.10
R Middle occipital gyrus	19		32	–66	40	3.95
R Middle occipital gyrus	19		33	–76	33	3.52
L Hippocampus	–	565	–20	–21	–14	4.02
L Amygdala	–		–27	–4	–17	3.53

This observation of subliminal priming effects only subsequent to the semantic, but not subsequent to the perceptual induction task was further confirmed in a formal interaction analysis crossing the factors induction task and semantic relatedness. As shown in Fig. 3 and Table II, semantic priming was significantly greater under Sem relative to Per in left vOT (FFG/ITG/IOG; BA 37), right vOT (ITG only; BA 37), in the right LG (BA 18), in the left anterior IFG (BA 45) and a bordering portion of the anterior insula, and in the right anterior IFG (BA 45). The opposite interaction effect (greater priming under Per relative to Sem) did not yield significant results neither at the voxel nor at the cluster level.

Functional connectivity of left ventral occipito-temporal cortex with other brain regions as a function of induction task

The dynamic functional networks theory proposes that attentional sensitization of unconscious cognition is implemented by a dynamic modulation of the functional communication between brain regions, depending on task sets. To specifically test this idea, we examined whether left vOT was differentially functionally connected with semantic versus perceptual brain regions in the corresponding induction task conditions. The present functional connectivity analyses focused on left vOT as seed region because

this area was consistently involved in subliminal semantic priming in the present and in earlier work (Ulrich et al., 2013).

We found that under semantic relative to perceptual induction left vOT showed stronger functional connectivity with an anterior part of the left superior frontal gyrus (SFG; BA 10; see Fig. 4, top right, and Table III). Functional connectivity with left vOT dramatically changed during perceptual induction (see Fig. 4, bottom right, and Table III): Compared with semantic induction, functional connectivity was increased with right-hemispheric, predominantly visual-perceptual brain regions: the IOG (BA 19), the LG (BA 17), the FFG (BA 37), the ITG (BA 37), the posterior MTG (BA 37), and the precuneus (BA 5). Outside the visual system, functional connectivity of left vOT was increased with the right hippocampus, and with the right anterior IFG (BA 45).

Finally, we tested whether this differential functional connectivity pattern as a function of induction task was related to the magnitude of priming. Significant correlations between the functional connectivity profile and priming would strongly support our proposal that a differential coupling of brain areas induced by task sets is an important mechanism underlying attentional control of unconscious processing. To this end, correlations between modulations of functional connectivity in the clusters obtained in the connectivity analyses (Sem > Per, or Per > Sem) and modulations of

Figure 3.

Brain regions demonstrating significantly greater priming after semantic (Sem) than after perceptual (Per) induction, overlaid on coronal sections of the group averaged T1 image. White numbers refer to the y -coordinates in MNI space. The bottom row depicts magnitude of neural activity, as represented by clus-

ter averaged parameter estimates associated with related, and unrelated trials under Sem, and Per. Error bars represent standard error of the mean (23 subjects). Abbreviations: a.u.: arbitrary unit, L: left, R: right, IFG: inferior frontal gyrus, LG: lingual gyrus, vOT: ventral occipito-temporal cortex.

priming at the behavioral, and neural level (i.e., priming_{Sem} minus priming_{Per}) were determined. For both behavioral and neural priming scores, a positive value indicates greater priming under Sem than under Per, a negative value indexes greater priming under Per than under Sem. With regard to behavioral priming, the increase in left vOT's functional connectivity with right IOG during perceptual induction was significantly correlated with the reduction in RT priming in this induction task condition (see Fig. 5A). Regarding neural priming, the increase in left vOT's functional connectivity with the right IFG/ITG, and with the right precuneus upon perceptual relative to semantic induction was associated with decreased priming in left vOT (see Fig. 5C), and in

right vOT (see Fig. 5D), respectively, under perceptual induction. Furthermore, increased functional connectivity between left vOT and left SFG upon semantic compared to perceptual induction was positively related to enhanced neural priming in the right lingual gyrus during semantic relative to perceptual induction (see Fig. 5B).

DISCUSSION

Traditionally, an unconsciously perceived stimulus is thought to trigger processes in the corresponding neural circuits independently of higher-level attentional

TABLE II. Brain regions bearing effects of significantly greater subliminal semantic priming subsequent to the semantic than to the perceptual induction task

Region	BA	Number of voxels	Peak voxel			
			x	y	z	z score
L Inferior frontal gyrus triangular part	45	168	-33	35	12	4.52
L Anterior Insula	-		-30	30	10	3.83
L Inferior temporal gyrus	37	142	-50	-57	-14	4.27
L Fusiform gyrus	37		-45	-57	-15	4.08
L Inferior occipital gyrus	37		-51	-61	-12	4.01
R Inferior frontal gyrus triangular part	45	205	39	27	19	4.01
R Lingual gyrus	18	128	11	-88	-3	3.79
R Inferior temporal gyrus	37	126	47	-54	-12	3.27

Figure 4.

Functional connectivity results. The coronal sections on the left show the locations of the 23 subject-wise seed voxels within left ventral occipito-temporal cortex (vOT). For each subject, the seed was defined as the peak voxel showing the maximal effect of greater semantic priming after semantic (Sem) relative to perceptual (Per) induction within the left vOT cluster obtained in the group analysis (see Table II). The sections on the right depict clusters with which left vOT was more strongly coupled under Sem than under Per (top right) or vice versa (bottom right).

White numbers refer to the y-coordinates in MNI space. The bottom row shows magnitude of functional connectivity with left vOT, as represented by cluster averaged parameter estimates. Error bars represent standard error of the mean (23 subjects). Abbreviations: a.u.: arbitrary unit, L: left, R: right, FFG: fusiform gyrus, IOG: inferior occipital gyrus, ITG: inferior temporal gyrus, LG: lingual gyrus, MTG: middle temporal gyrus, SFG: superior frontal gyrus.

influences. In challenging this classical view, we tested in an fMRI study a novel theoretical framework suggesting that attentional sets orchestrate processing pathways by dynamically establishing large-scale functional networks and thus influence stimulus processing even under unconscious viewing conditions.

In support of this dynamic functional networks theory, we found that only subsequent to an activated semantic task set masked word primes were able to modulate activity within a distributed semantic brain network including vOT and IFG, which has been shown to support both conscious (Gold et al., 2006, 2009; Ulrich et al., 2013; Wheatley et al., 2005) and unconscious semantic processing (Ulrich

et al., 2013). Under a perceptual task set neural priming in these semantic pathways was attenuated and did not reach statistical significance. These results show that unconscious semantic processing crucially depends on sensitization of corresponding processing pathways by a semantic task set (Kiefer and Martens, 2010). Thus, unconscious cognition is not autonomous as traditionally thought (Heil et al., 2004; Neely and Kahan, 2001; Posner and Snyder, 1975; Schneider and Shiffrin, 1977). The present findings extend previous behavioral and electrophysiological subliminal priming studies (Adams and Kiefer, 2012; Kiefer and Martens, 2010; Martens et al., 2011; Martens and Kiefer, 2009) by localizing these attentional effects on subliminal

TABLE III. Brain regions showing differential functional connectivity with left vOT under conditions of semantic versus perceptual induction

Region	BA	Number of voxels	Peak voxel			
			<i>x</i>	<i>y</i>	<i>z</i>	<i>z</i> score
Semantic induction > Perceptual induction						
L Superior frontal gyrus	10	67	-24	60	24	3.73
Perceptual induction > Semantic induction						
R Precuneus	5	445	11	-48	63	4.26
R Fusiform gyrus	37	293	42	-45	-11	4.07
R Inferior temporal gyrus	37		57	-55	-5	3.36
R Inferior frontal gyrus triangular part	45	83	38	29	13	4.02
R Lingual gyrus	17	128	6	-79	-5	3.81
R Hippocampus	-	52	33	-18	-12	3.70
R Inferior occipital gyrus	19	67	38	-76	-5	3.54
R Middle temporal gyrus	37	107	53	-61	9	3.38
R Middle temporal gyrus	37		44	-66	18	3.32

semantic processing to established semantic brain areas: While vOT as a region of the ventral visual stream has been suggested to code visual conceptual features (Barsalou et al., 2003; Chao et al., 1999; Kiefer and Barsalou, 2013; Kiefer and Pulvermüller, 2012; Martin, 2007; Martin and Chao, 2001), the IFG has been associated with semantic retrieval processes such as meaning selection (Cardillo et al., 2004; Thompson-Schill et al., 1997). Hence, our neuroimaging findings provide direct evidence that semantic versus perceptual task sets determine to which extent a subliminal prime is processed within cortical semantic networks.

The question arises whether the modulation of priming as a function of induction task is reflecting that the semantic induction task has a true facilitating effect on semantic priming as compared to no induction task, or that the perceptual induction task is hampering semantic priming due to the need of switching processing pathways.

Task switching is indeed an important issue to consider. However, we do not think that the attenuated semantic priming effects after perceptual induction were observed merely due to switching costs since such effects played a role under both induction tasks. Under Per, switching was required from a perceptual shape decision task to a lexical decision task. Under Sem, subjects had to switch from a semantic living/nonliving decision task to the lexical decision task. One might think that task switching operations were required to a lesser extent under Sem than under Per, given that both the induction task and the lexical decision task probed semantic processing. There is evidence, however, that similar task sets cause even greater switching costs than dissimilar task sets, in particular at the motor level (Gade and Koch, 2007). Thus, task switching effects have certainly played a role in our study but, importantly, they had an effect under both induction tasks, thereby likely not compromising our interpretations. Our claim is furthermore supported by the lack of a behavioral

main effect of induction task ($F(1, 22) = 0.12$, $P = 0.738$) suggesting comparable overall switching costs.

When one would like to assess whether semantic induction increases priming compared with no induction, our previous investigation (Ulrich et al., 2013) might be a reference study, although a direct comparison is difficult due to slight methodological differences. Furthermore, inclusion of an induction task imposes a task switching component in addition to reducing attentional capacity available for masked prime processing (Martens and Kiefer, 2009). A comparison of the magnitudes [arbitrary unit] of the cluster-averaged parameter estimates representing vOT activation for R and U under subliminal conditions reveals the following pattern: In our previous study, the parameter estimates were 3.68 for R, and 4.12 for U, resulting in a priming difference of 0.44. The facilitation of R relative to U thus amounts to about 11%. In the present study, the parameter estimates were 4.50 for R, and 5.70 for U, yielding a priming effect of 1.20 which corresponds to a 21 % facilitation of R compared to U. The comparison indicates a facilitating influence of the semantic induction task on semantic priming. Priming at the reaction time level, in the first place, would be at odds with that interpretation however, given a subliminal priming effect of 27 ms in our previous study, and 22 ms under Sem in the present investigation. However, as mentioned above, an induction task reduces attentional capacity and is very likely to introduce switching costs as a consequence of switching between the induction task and the lexical decision task. It is well conceivable that, at the same time, the semantic induction task facilitated priming in semantic pathways (indicated by greater neural priming in vOT) compared with no induction task but, due to task switching, led to inhibitory effects at subsequent processing stages (e.g., at the motor level), thereby resulting in an overall reduction in reaction time priming, the latter being the sum of both facilitatory and inhibitory effects. In summary, we argue

Figure 5.

Correlations across participants between differences in functional connectivity (FC) after semantic (Sem) versus perceptual (Per) induction, and modulation of behavioral (A) or neural semantic priming (B–D). Modulation of semantic priming, represented by the y-axes, was defined as the difference “priming_{Sem} minus priming_{Per}”, that is, a positive value indicates greater priming under Sem than under Per, and a negative value the opposite, that is, greater priming under Per than under Sem. A positive correlation between FC and priming measures therefore indicates that increased FC was associated with greater priming under Sem than under Per. The correlation analyses were performed voxel-wise within the clusters bearing significant differences in functional connectivity with left vOT under Sem versus Per, listed in Table III. Estimates of neural priming modulation had been obtained subject-wise by extracting and cluster-averaging the parameter estimates representing neural activity associated with related, and unrelated trials under Sem, and Per, and subsequent computation of the difference “ U_{Sem} minus R_{Sem} minus U_{Per} plus R_{Per} ”, from three brain regions showing greater

semantic priming under Sem relative to Per (i.e., the right lingual gyrus, and left, and right ventral occipito-temporal cortex, see also Table II). Each scatter plot refers to the peak voxel exhibiting the highest correlation in the respective analysis. Pearson correlation coefficients for the peak voxel, and for the mean across all significant voxels are given above the scatter plots. Significance was assessed at $P < 0.05$, one-sided. The correlations suggest that the stronger vOT was coupled with the perceptual network in the perceptual (induction) task (panels A, C, D), the more semantic priming was attenuated under Per compared with Sem, that is, greater priming under Sem than under Per. Likewise, the stronger vOT was coupled with the semantic network under Sem (panel B), the more semantic priming was increased under Sem compared with Per. Abbreviations: a.u.: arbitrary unit, ms: milliseconds, L: left, R: right, FFG: fusiform gyrus, IOG: inferior occipital gyrus, ITG: inferior temporal gyrus, LG: lingual gyrus, SFG: superior frontal gyrus, vOT: ventral occipito-temporal cortex.

in favor of the interpretation that enhanced priming effects under Sem have likely been the result of facilitation or sensitization of semantic pathways rather than the reflection of greater task switching demands under Per.

Importantly, as predicted by the dynamic functional networks theory, the semantic and the perceptual induction tasks were associated with differential functional connectivity profiles. Greater functional connectivity between left vOT and left SFG under semantic relative to perceptual induction is in good accordance with previous reports associating the SFG with semantic retrieval (e.g., Binder et al., 1997, 1999; Whitney et al., 2011). Hence, during a semantic induction task, left vOT is more strongly functionally coupled with a semantic retrieval network compared with perceptual induction. Conversely, under perceptual compared with semantic induction, functional connectivity of vOT was greater with several brain regions of the ventral visual pathway typically involved in object recognition (e.g., Gauthier et al., 1997; Haxby et al., 1991, 1994; Ishai et al., 1999; for reviews, see Grill-Spector, 2003, and Grill-Spector and Malach, 2004). More specifically, the IOG cluster corresponds to a part of the so called “lateral occipital complex” (Malach et al., 1995), well known for its involvement in shape processing (Cant et al., 2009; Cant and Goodale, 2007; Denys et al., 2004; Kourtzi and Kanwisher, 2000; Murray et al., 2003; Schultz et al., 2008). Hence, during the perceptual induction task, left vOT was more strongly coupled with visual perceptual brain regions. Most importantly, this task set induced functional connectivity pattern has a functional relevance for orchestrating the unconscious processing streams: We showed that the interindividual modulation of functional connectivity determined the magnitude of behavioral and neural priming in the different induction task conditions. When regressing the modulation of priming effects by induction tasks to the functional connectivity profile of left vOT, the extent of left vOT’s integration into a semantic versus perceptual network during the corresponding induction tasks predicted the magnitude differences in behavioral and neural semantic priming under semantic versus perceptual induction.

The present functional connectivity findings support the dynamic functional networks theory and considerably advance our understanding of the mechanisms underlying attentional control of unconscious processing at the systems level: They show that semantic versus perceptual task sets establish temporary functional networks by differentially coupling brain areas even across long distances. The nature of these temporary functional networks, in turn, determines along which pathways an unconscious stimulus is processed.

Therefore, we suggest that a given brain region’s precise function may be determined by its temporary, dynamic coupling with other brain areas into large-scale functional networks. In the present study, when participants performed the semantic induction task, left vOT likely became integrated into a “semantic network”, as evidenced by its

increased functional connectivity with the left superior frontal gyrus upon semantic relative to perceptual induction. We assume that, thereby, a semantic function was conferred to left vOT making it sensitive to semantic activation. Thus, the subsequent subliminally presented prime could be processed at the semantic level and, as a consequence, influenced processing of the visible targets of the upcoming lexical decision task, as reflected in behavioral and neural semantic priming effects. In contrast, upon the perceptual induction task, the brain system was appropriately configured to carry out the shape classification task, reflected by increased functional connectivity of left vOT with regions known to be involved in shape processing such as the IOG (e.g., Gauthier et al., 1997; Grill-Spector, 2003; Grill-Spector and Malach, 2004; Haxby et al., 1991, 1994; Ishai et al., 1999). Due to integration into a “perceptual network”, left vOT probably served a perceptual function, thus biasing subsequent unconscious information processing towards the dimension “shape”, and reducing left vOT’s sensitivity to semantic activation. Hence, after perceptual relative to semantic induction, semantic processing of the primes in vOT was less pronounced resulting in attenuated subliminal semantic priming. In support of this proposal, a perceptual task set that focuses on shape boosted form-based subliminal visuo-motor priming as shown previously (Martens et al., 2011; Zovko and Kiefer, 2013). Complementary findings outside the field of priming have recently been obtained by Heinzle et al. (2012) with a cued visuo-motor response task which required interaction between visual and motor areas either within or across hemispheres. Using a multivariate classification approach for fMRI data analysis it could be shown that, depending on the task set, functional connectivity changed within a bilateral large-scale brain network comprising primary and extrastriate visual cortex as well as primary motor and premotor cortex.

The present dynamic functional networks account implies that a given brain area may serve different functions depending on its task set-driven integration into temporary functional networks. This framework can therefore explain frequently observed contradictory findings across studies regarding the function of one and the same brain region (for a review, see Cabeza and Nyberg, 2000). As the experimental task necessarily differs between studies investigating different functions, so does the task set prepared to adequately perform the respective task. Since the specific task set, in turn, determines the coupling of a particular brain region of interest with a larger functional network, the function of the former may vary depending on the activated task set. Therefore, the present research emphasizes the flexibility of a brain region’s function and emphasizes the necessity to characterize the function of brain areas at the systems level by determining its coupling with large-scale functional networks. As the temporal resolution of fMRI is low and does not allow separation of activity in time associated with the induction task, and with the primed lexical decision task, it would be interesting to determine in future studies how

functional connectivity of a given brain region such as vOT unfolds over time using more time sensitive measures of brain activity such as scalp or intracranial electrophysiological recordings.

In conclusion, the present results specify the neurobiological mechanisms underlying attentional control of unconscious cognition. We show that a subliminally presented masked prime modulates activity within a network of brain areas known to support semantic processing only when a semantic task set is active. A perceptual task set attenuates unconscious semantic processing within this cortical network. This attentional control of unconscious semantic processing is established by a temporary and dynamic integration of brain areas into different functional networks depending on the active task set. Our research provides important insight into the adaptability of the human brain in orchestrating the flow of unconscious information in the processing streams to support goal-related interactions with the dynamically changing challenges of the environment.

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REFERENCES

- Adams SC, Kiefer M (2012): Testing the attentional boundary conditions of subliminal semantic priming: The influence of semantic and phonological task sets. *Front Hum Neurosci* 6: 241.
- Ansorge U, Horstmann G, Scharlau I (2011): Top-down contingent feature-specific orienting with and without awareness of the visual input. *Adv Cogn Psychol* 7:108–119.
- Ansorge U, Neumann O (2005): Intentions determine the effect of invisible metacontrast-masked primes: Evidence for top-down contingencies in a peripheral cuing task. *J Exp Psychol Hum Percept Perform* 31:762–777.
- Barsalou LW, Kyle Simmons W, Barbey AK, Wilson CD (2003): Grounding conceptual knowledge in modality-specific systems. *Trends Cogn Sci* 7:84–91.
- Binder JR, Frost JA, Hammeke TA, Bellgowan PS, Rao SM, Cox RW (1999): Conceptual processing during the conscious resting state: A functional MRI study. *J Cogn Neurosci* 11:80–95.
- Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T (1997): Human brain language areas identified by functional magnetic resonance imaging. *J Neurosci* 17:353–362.
- Breitmeyer BG, Ögmen H. 2006. Visual masking: Time slices through conscious and unconscious vision. Oxford (UK): Oxford University Press.
- Bressler SL, Kelso JA (2001): Cortical coordination dynamics and cognition. *Trends Cogn Sci* 5:26–36.
- Cabeza R, Nyberg L (2000): Imaging cognition II: An empirical review of 275 PET and fMRI studies. *J Cogn Neurosci* 12:1–47.
- Cant JS, Arnott SR, Goodale MA (2009): fMR-adaptation reveals separate processing regions for the perception of form and texture in the human ventral stream. *Exp Brain Res* 192:391–405.
- Cant JS, Goodale MA (2007): Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cereb Cortex* 17:713–731.
- Cardillo ER, Aydelott J, Matthews PM, Devlin JT (2004): Left inferior prefrontal cortex activity reflects inhibitory rather than facilitatory priming. *J Cogn Neurosci* 16:1552–1561.
- Chao LL, Haxby JV, Martin A (1999): Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nat Neurosci* 2:913–919.
- Copland DA, de Zubicaray GI, McMahon K, Wilson SJ, Eastburn M, Chenery HJ (2003): Brain activity during automatic semantic priming revealed by event-related functional magnetic resonance imaging. *NeuroImage* 20:302–310.
- Dale AM (1999): Optimal experimental design for event-related fMRI. *Hum Brain Mapp* 8:109–114.
- Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C (2006): Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends Cogn Sci* 10:204–211.
- Dehaene S, Naccache L, Le Clec HG, Koechlin E, Mueller M, Dehaene-Lambertz G, van de Moortele PF, Le Bihan D (1998): Imaging unconscious semantic priming. *Nature* 395:597–600.
- Denys K, Vanduffel W, Fize D, Nelissen K, Peuskens H, Van Essen D, Orban GA (2004): The processing of visual shape in the cerebral cortex of human and nonhuman primates: A functional magnetic resonance imaging study. *J Neurosci* 24:2551–2565.
- Fox MD, Liu H, Pascual-Leone A (2013): Identification of reproducible individualized targets for treatment of depression with TMS based on intrinsic connectivity. *NeuroImage* 66C:151–160.
- Fries P (2005): A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends Cogn Sci* 9:474–480.
- Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, Dolan RJ (1997): Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage* 6:218–229.
- Gade M, Koch I (2007): The influence of overlapping response sets on task inhibition. *Mem Cognit* 35:603–609.
- Gauthier I, Anderson AW, Tarr MJ, Skudlarski P, Gore JC (1997): Levels of categorization in visual recognition studied using functional magnetic resonance imaging. *Curr Biol* 7:645–651.
- Giesbrecht B, Camblin CC, Swaab TY (2004): Separable effects of semantic priming and imageability on word processing in human cortex. *Cereb Cortex* 14:521–529.
- Gold BT, Andersen AH, Jicha GA, Smith CD (2009): Aging influences the neural correlates of lexical decision but not automatic semantic priming. *Cereb Cortex* 19:2671–2679.
- Gold BT, Balota DA, Jones SJ, Powell DK, Smith CD, Andersen AH (2006): Dissociation of automatic and strategic lexical-semantics: Functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *J Neurosci* 26:6523–6532.
- Green DM, Swets JA. 1966. Signal detection theory and psychophysics. New York (NY): Wiley.
- Greenwald AG, Draine SC, Abrams RL (1996): Three cognitive markers of unconscious semantic activation. *Science* 273:1699–1702.

- Grill-Spector K (2003): The neural basis of object perception. *Curr Opin Neurobiol* 13:159–166.
- Grill-Spector K, Malach R (2004): The human visual cortex. *Annu Rev Neurosci* 27:649–677.
- Haxby JV, Grady CL, Horwitz B, Ungerleider LG, Mishkin M, Carson RE, Herscovitch P, Schapiro MB, Rapoport SI (1991): Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proc Natl Acad Sci USA* 88:1621–1625.
- Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL (1994): The functional organization of human extrastriate cortex: A PET-rCBF study of selective attention to faces and locations. *J Neurosci* 14:6336–6353.
- Heil M, Rolke B, Pecchinenda A (2004): Automatic semantic activation is no myth: Semantic context effects on the N400 in the letter-search task in the absence of response time effects. *Psychol Sci* 15:852–857.
- Heinze J, Wenzel MA, Haynes JD (2012): Visuomotor functional network topology predicts upcoming tasks. *J Neurosci* 32:9960–9968.
- Holender D (1986): Semantic activation without conscious identification in dichotic listening, parafoveal vision, and visual masking: A survey and appraisal. *Behav Brain Sci* 9:1–66.
- Ishai A, Ungerleider LG, Martin A, Schouten JL, Haxby JV (1999): Distributed representation of objects in the human ventral visual pathway. *Proc Natl Acad Sci USA* 96:9379–9384.
- Kentridge RW, Heywood CA, Weiskrantz L (2004): Spatial attention speeds discrimination without awareness in blindsight. *Neuropsychologia* 42:831–835.
- Kiefer M (2002): The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Cogn Brain Res* 13:27–39.
- Kiefer M (2012): Executive control over unconscious cognition: Attentional sensitization of unconscious information processing. *Front Hum Neurosci* 6:61.
- Kiefer M, Barsalou LW (2013): Grounding the human conceptual system in perception, action, and internal states. In: Prinz W, Beisert M, Herwig A, editors. *Action science: Foundations of an emerging discipline*. Cambridge (UK): MIT Press.
- Kiefer M, Brendel D (2006): Attentional modulation of unconscious "automatic" processes: Evidence from event-related potentials in a masked priming paradigm. *J Cogn Neurosci* 18:184–198.
- Kiefer M, Martens U (2010): Attentional sensitization of unconscious cognition: Task sets modulate subsequent masked semantic priming. *J Exp Psychol Gen* 139:464–489.
- Kiefer M, Pulvermüller F (2012): Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. *Cortex* 48:805–825.
- Kiefer M, Sim EJ, Helbig H, Graf M (2011): Tracking the time course of action priming on object recognition: Evidence for fast and slow influences of action on perception. *J Cogn Neurosci* 23:1864–1874.
- Kiefer M, Spitzer M (2000): Time course of conscious and unconscious semantic brain activation. *Neuroreport* 11:2401–2407.
- Kotz SA, Cappa SF, von Cramon DY, Friederici AD (2002): Modulation of the lexical-semantic network by auditory semantic priming: An event-related functional MRI study. *NeuroImage* 17:1761–1772.
- Kourtzi Z, Kanwisher N (2000): Cortical regions involved in perceiving object shape. *J Neurosci* 20:3310–3318.
- Kunde W, Reuss H, Kiesel A (2012): Consciousness and cognitive control. *Adv Cogn Psychol* 8:9–18.
- Lau HC, Passingham RE (2007): Unconscious activation of the cognitive control system in the human prefrontal cortex. *J Neurosci* 27:5805–5811.
- Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB (1995): Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci U S A* 92:8135–8139.
- Martens U, Ansorge U, Kiefer M (2011): Controlling the unconscious: Attentional task sets modulate subliminal semantic and visuomotor processes differentially. *Psychol Sci* 22:282–291.
- Martens U, Kiefer M (2009): Specifying attentional top-down influences on subsequent unconscious semantic processing. *Adv Cogn Psychol* 5:56–68.
- Martin A (2007): The representation of object concepts in the brain. *Annu Rev Psychol* 58:25–45.
- Martin A, Chao LL (2001): Semantic memory and the brain: Structure and processes. *Curr Opin Neurobiol* 11:194–201.
- Martin A, Haxby JV, Lalonde FM, Wiggs CL, Ungerleider LG (1995): Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270:102–105.
- Matsumoto A, Iidaka T, Haneda K, Okada T, Sadato N (2005): Linking semantic priming effect in functional MRI and event-related potentials. *NeuroImage* 24:624–634.
- Mattler U (2003): Priming of mental operations by masked stimuli. *Percept Psychophys* 65:167–187.
- McLaren DG, Ries ML, Xu G, Johnson SC (2012): A generalized form of context-dependent psychophysiological interactions (gPPI): A comparison to standard approaches. *NeuroImage* 61:1277–1286.
- Meyer DE, Schvaneveldt RW (1971): Facilitation in recognizing pairs of words: Evidence of a dependence between retrieval operations. *J Exp Psychol* 90:227–234.
- Miller EK, Cohen JD (2001): An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24:167–202.
- Mueller S, Wang D, Fox MD, Yeo BT, Sepulcre J, Sabuncu MR, Shafee R, Lu J, Liu H (2013): Individual variability in functional connectivity architecture of the human brain. *Neuron* 77:586–595.
- Murray SO, Olshausen BA, Woods DL (2003): Processing shape, motion and three-dimensional shape-from-motion in the human cortex. *Cereb Cortex* 13:508–516.
- Naccache L, Blandin E, Dehaene S (2002): Unconscious masked priming depends on temporal attention. *Psychol Sci* 13:416–424.
- Neely JH (1991): Semantic priming effects in visual word recognition: A selective review of current findings and theories. In: Besner D, Humphreys GW, editors. *Basic processes in reading: Visual word recognition*. Hillsdale (NJ): Lawrence Erlbaum Associates. p 264–336.
- Neely JH, Kahan TA (2001): Is semantic activation automatic? A critical re-evaluation. In: Roediger HL, Nairne JS, Neath I, Suprenant AM, editors. *The Nature of Remembering: Essays in Honor of Robert G. Crowder*. Washington (DC): American Psychological Association. p 69–93.
- Posner MI, Snyder CRR (1975): Attention and cognitive control. In: Solso RL, editor. *Information Processing and Cognition: The Loyola Symposium*. Hillsdale (NJ): Lawrence Erlbaum Associates. p 55–85.

- Rissman J, Eliassen JC, Blumstein SE (2003): An event-related fMRI investigation of implicit semantic priming. *J Cogn Neurosci* 15:1160–1175.
- Ruoff A. 1990. Häufigkeitswörterbuch gesprochener Sprache. Tübingen (Germany): Niemeyer.
- Sakai K, Passingham RE (2003): Prefrontal interactions reflect future task operations. *Nat Neurosci* 6:75–81.
- Schmidt F, Haberkamp A, Schmidt T (2011): Dos and don'ts in response priming research. *Adv Cogn Psychol* 7:120–131.
- Schneider W, Shiffrin RM (1977): Controlled and automatic human information processing: I. Detection, search, and attention. *Psychol Rev* 84:1–66.
- Schultz J, Chuang L, Vuong QC (2008): A dynamic object-processing network: Metric shape discrimination of dynamic objects by activation of occipitotemporal, parietal, and frontal cortices. *Cereb Cortex* 18:1302–1313.
- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ (1997): Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proc Natl Acad Sci USA* 94:14792–14797.
- Ulrich M, Hoenig K, Grön G, Kiefer M (2013): Brain activation during masked and unmasked semantic priming: Commonalities and differences. *J Cogn Neurosci* 25:2216–2229.
- Vorberg D, Mattler U, Heinecke A, Schmidt T, Schwarzbach J (2003): Different time courses for visual perception and action priming. *Proc Natl Acad Sci USA* 100:6275–6280.
- Wheatley T, Weisberg J, Beauchamp MS, Martin A (2005): Automatic priming of semantically related words reduces activity in the fusiform gyrus. *J Cogn Neurosci* 17:1871–1885.
- Whitney C, Jefferies E, Kircher T (2011): Heterogeneity of the left temporal lobe in semantic representation and control: Priming multiple versus single meanings of ambiguous words. *Cereb Cortex* 21:831–844.
- Wible CG, Han SD, Spencer MH, Kubicki M, Niznikiewicz MH, Jolesz FA, McCarley RW, Nestor P (2006): Connectivity among semantic associates: An fMRI study of semantic priming. *Brain Lang* 97:294–305.
- Womelsdorf T, Fries P (2007): The role of neuronal synchronization in selective attention. *Curr Opin Neurobiol* 17:154–160.
- Zovko M, Kiefer M (2013): Do different perceptual task sets modulate electrophysiological correlates of masked visuomotor priming? Attention to shape and color put to the test. *Psychophysiology* 50:149–157.